ECOLOGICAL EFFECTS OF FIRE ON NORTH SWEDISH FORESTS

BY

EVALD UGGLA

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ALMQVIST & WIKSELLS BOKTRYCKERI AB

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INAUGURAL DISSERTATION

by

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FIL. LIC., ÖSTG.

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PREFACE

This paper is a brief summary of some results of my investigations concerning the effect of fire on forest vegetation and humus cover. These studies have, with several interruptions, been carried on since 1945. Most of the investigations have been performed in Muddus National Park which is situated in Lapland just north of the Arctic Circle.

The controlled burnings frequently applied in present-day silviculture supply an excellent opportunity for studies of the events during and immediately after a fire. For this reason it appeared suitable to link the long-term investigations in Muddus with experimental studies during controlled burnings. These studies were carried out in forests in Hälsingland, owned by the AB Iggesunds Bruk, who provided every facility for the investigations.

The papers cited below have for the greatest part been prepared at the Institute of Plant Ecology, Royal University of Uppsala. Professor G. Einar Du Rietz has put the resources of the Institute at my disposal, and I am most grateful for his personal guidance and enthusiastic encouragement. Dr. Tore Arnborg, who from the start was the leader of the scientific investigations in Muddus, introduced me to this interesting problem as early as 1945. In the course of the years he has given me inestimable support, always showing stimulating interest in this work. Dr. Gustaf Sirén and Dr. Hugo Sjörs have also read and criticized the manuscripts, and during discussions with them I have profited greatly from their knowledge.

With particular gratitude I think of good companions during the field work in the primeval forests, and especially of my wife who undauntedly assisted me during our stay in the often inhospitable burnt areas.

To them and to other persons named in earlier papers, I wish to express my most sincere gratitude.

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Evald Uggla

INTRODUCTION

The present paper is a summary of the following investigations by the author:

I. En vegetationsprofil på skogsbrandfält i Muddus nationalpark. English summary: A vegetation analysis in a burnt forest area in the Muddus National Park. *Sv. bot. tidskr.*, 43. Uppsala, 1949.

II. Mark- och lufttemperaturer vid hyggesbränning samt eldens inverkan på vegetation och humus. English summary: Temperatures during controlled burning. The effect of the fire on the vegetation and the humus cover. *Norrl. skogsvårdsförb. tidskr.*, IV. Stockholm, 1957.

III. Skogsbrandfält i Muddus nationalpark. English summary: Forest fire areas in Muddus National Park, Northern Sweden. *Acta Phytogeogr. Suec.*, 41. Uppsala, 1958.

Of these papers, No. II is an experimental study performed in connection with controlled burnings in the province of Hälsingland, lat. 61°30′ N and long. 15°30′ E. The object was to measure the temperatures that occur in the humus cover and in the air during burning, and to ascertain the effect of the fire on the vegetation and the humus cover. Measurements of this type have not earlier been made in Sweden and can be of importance for forestry. The cut, and later burnt, areas had been covered chiefly with *Picea abies*, with an inactive raw humus cover.

Nos. I and III are studies of the regeneration of vegetation in forest fire areas within the largest reserve of primeval forest in Sweden, the Muddus National Park. This reserve, which covers about 50,000 hectares (123,500 acres), is situated about 600 km north of Hälsingland, lat. 66°55′ N and long. 20°10′ E (central part).

Fire has always been a very important factor in determining the extent and composition of boreal forests. Even during recent centuries most woodlands have been subjected to fire in one form or another—forest fires, burning for crops practised in former times and the present-day controlled burning. Almost everywhere one can find charcoal in the humus layer as evidence of fire.

In former times vast areas could be devastated by forest fires but in our days the forest fire areas have decreased. In Muddus National Park we still have the opportunity to follow the undisturbed succession of vegetation after forest fires. The burnt areas in-

vestigated by the author within this reserve of coniferous forest are from the years 1920, 1933, 1941, and 1947. They represent different forest-site types.

During the present century, fire has been used to an increasing extent in the service of silviculture, especially in the northern parts of Sweden. Controlled burning is practised on raw humus grounds, mainly at high levels. It is now generally agreed that a properly conducted, controlled burning on ground that is not too dry is the most efficient method of activating the humus, and of reducing the labour difficulties in planting and sowing on such land.

The circumstance that fire has come into increasing use in the forestry is due to several cooperating factors some of which will here be briefly dealt with.

After the passage of fire over the humus cover, the ashes and carbonized remains of the living vegetation and the litter form a thin cover upon the otherwise undamaged humus layer. The alkalis of the ash can then be absorbed by the humus cover in an easily accessible form, the nitrogen metabolism is increased, and the conditions for most micro-organisms are ameliorated. The destruction of the previous vegetation has reduced the root competition. The temperature at the surface of the soil will rise on account of the increased ability of heat absorption of the black humus cover, which favours the germination of seeds.

The fire has an indirectly favourable influence also in the long run by favouring the entry of birch and aspen as pioneer trees into the burnt areas. The leaves contribute every year a new quantity of litter to the soil, the temperature of which rises below the leafless trees in the spring. In a clearing the density of the humus cover diminishes, through, amongst other things, the soil temperature rising and the precipitation having greater opportunity to percolate down to the root system (ARNBORG 1951).

A feeble forest fire, on not too dry raw humus ground, can be compared with a controlled burning, but on poor, dry soils, uncontrolled forest fires can have devastating effects, as happened in 1933 in Muddus National Park. On such soils the activating effects of the fire soon disappear. Since also the addition of litter will be very inconsiderable for a long time, degeneration of the forest soil often results.

TEMPERATURES DURING CONTROLLED BURNING (II)

Soil temperature

The survival of vegetation and micro-organisms after a fire depends on the temperatures reached in the humus cover. The severity of the fire is dependent on several factors such as the forest type, the quantity and composition of combustible material, and the strength of the wind. The moisture content of the soil, particularly in the humus layer, is not the least important factor.

The temperature fluctuations were followed by direct reading on a resistance bridge provided with temperature pick-ups. The resistance bridge (Philips, Type RDM 15) is accurate to about 0.15°C and the pick-ups have a maximum error of 0.2 Ω, which corresponds with an accuracy of 0.12°C at 0°C. The total error for the pick-ups and the instrument is thus about 0.3°C. For measuring the high temperatures that occur at, and just above, the soil surface, a pick-up with a platinum element was necessary, while for lower temperatures—below 150°C—nickel elements were used.

A common feature of the measurements during controlled burnings was the low temperature in the humus cover as compared with that at the soil surface, which is illustrated in Fig. 1. Here it is also shown that the temperature at the soil surface on the day after the burn was rather high, owing to insolation heat absorbed in the charred layer. The curves also illustrate the characteristic displacement in time, which derives from the low thermal conductivity and high thermal capacity (specific heat) of the soil and its content of moisture.

In another test, however, the temperature at a depth of 3 cm remained at about 100°C for about 20 minutes and then dropped rapidly. In this test the fire was fairly intense and the humus cover was rather dry. The moisture content in the F-layer was 17.6 % before and 3.7 % after the burning. The long period at 100°C indicates that a zone of condensation was formed at this depth. The temperature rise was arrested in this zone owing to the need of heat for vaporization of the moisture condensed in the soil in the first phase of burning. Only after the water had been evaporated could the fire have a chance to go deeper, but at this time the fire front had passed the test plot, so that the temperature had begun to drop rapidly.

It is evident from the tests that the humus cover is an excellent thermal insulator, a fact that has often been pointed out. This is partly explained by the condensation of water vapour formed in the burning of organic matter that always occurs in the upper soil stratum during a burn. As the fire advances, the damp humus cover acts as a cold barrier, where moisture is condensed. Immediately below the fire zone there is thus a "sweating zone", which effectively prevents the fire from penetrating deeper into the humus cover. Before this can happen, the moisture must be evaporated.

During a feeble forest fire on not too dry soil, or a controlled burning, the high temperature does not as a rule last long enough for the moisture in the F-layer to evaporate. Only if the fire front is arrested, particularly on dry ground, is it likely that the humus cover will burn partly or completely. On moist sites the fire will usually consume only slash and litter, dried-out vegetation and possibly the uppermost dry part of the humus cover where air has free access.

Air temperature

During a forest fire or a controlled burning the crowns of the trees are often killed. The problem of resistance to heat and smoke is very complicated. Some data are provided

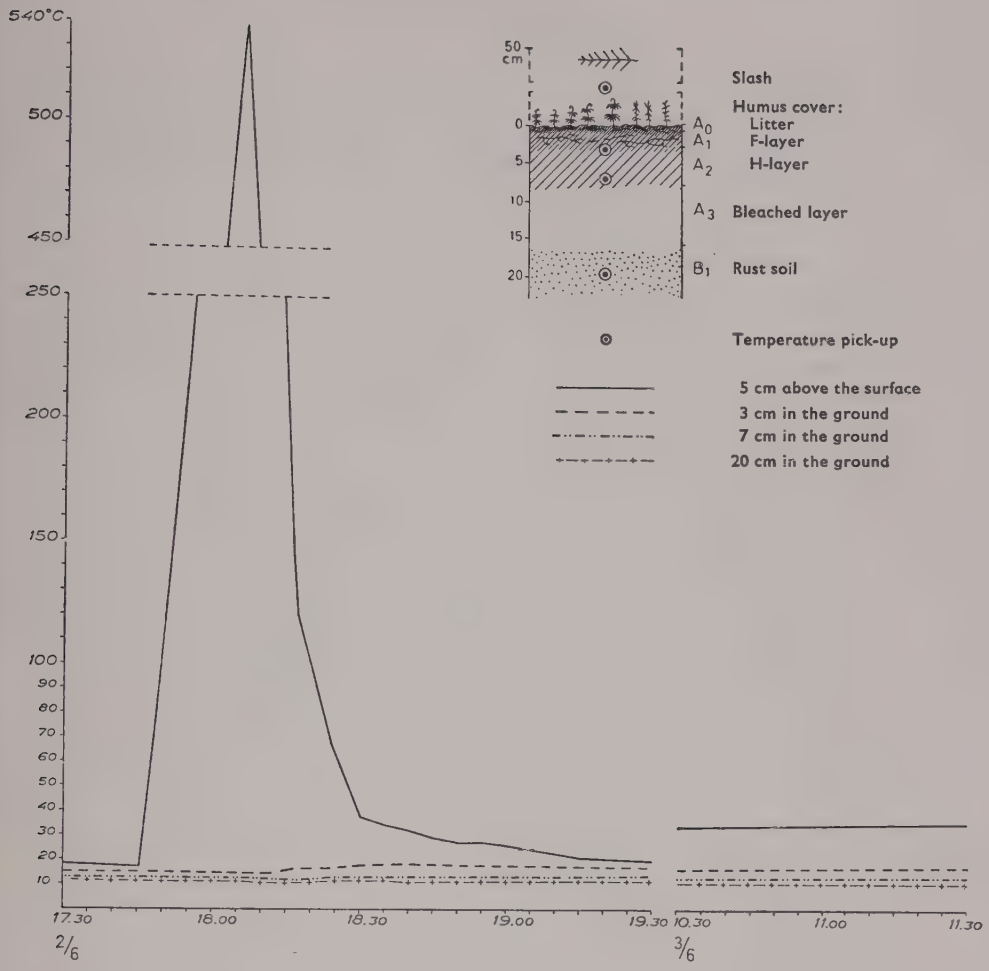

Fig. 1. An example of the high insulating capacity of the humus cover during a controlled burning (II p. 456). Comparison of the temperature curves the following day shows the heat absorption of the charred ground.

on the air temperature during a controlled burning in Hälsingland, which might serve as a basis for more thorough investigations.

Repeated measurements in open flames gave a temperature in the hottest part of about 1150°C. A radiation pyrometer with a temperature range between 600° and 2200°C was used. This type of instrument is also used at the Government Testing Laboratories. The high temperatures in the open flame are similar to those obtained in experiments

in fire prevention, in which temperatures of about 1000°C are reached indoors, and about 1300°C with an adequate air supply.

The temperature at the crowns is determined by absorption of heat radiated from the heart of the fire and by the temperature of the air–smoke mixture. As is well known, the temperature is highest when the smoke is yellowish-brown to black. The dark type of smoke is formed if combustion is incomplete, for example, when the fire front is so broad that the oxygen supply is insufficient, or when the combustible material is damp, or too plentiful for the available air.

Fig. 2 shows a diagram of a site of a controlled burning during which temperatures were measured at various levels on three experimental trees standing outside the fire lane. Hatching shows the fractions of the crowns that were found to be dead in June of the following year. For the measurement of the temperatures at the trees, maximum thermometers recording up to 300°C were used. The accuracy of these instruments was tested by the Government Testing Laboratories. During this burning the wind was strong and the smoke drove down below the crowns of the seed trees left on the cut and burnt area. Therefore no damage to these trees was observed. At the fire lane, however, the smoke hit the tree crowns, and the temperature was as high as 89°C at 12 m above the ground, while 68°C was recorded at the height of 3 m. If the wind is weak, however, the smoke will hit the crowns from below, and the temperature falls rapidly with height. In spite of the fact that the bark of an experimental tree was ignited, the temperature was 150°C at 6 m and only 45°C at 9 m above the ground. The needles of this tree were killed even at 9 m.

Only those parts of the crowns were killed which were engulfed by yellowish-brown to black smoke. Smoke which results from incomplete combustion thus seems to be dangerous for the needles. No damage was done by greyish-white condensation smoke.

THE EFFECT OF FIRE ON THE VEGETATION (I–III)

When the front of the fire has passed, there remains of the surface vegetation only a gray layer of ash mixed with completely or partially carbonized slash. As has been shown above, the temperature rises only slightly below the zone of condensation, in spite of the intense heat at the surface, provided that the fire has not been too severe. In cases where the front of the fire has moved continuously the humus cover is as a rule only slightly burnt, and in humid depressions the vegetation is often totally undamaged. From such spots regeneration on the burnt areas can start, as also from subterranean runners and seeds which have survived the fire in the humus cover.

The development of the primary succession depends on many cooperating factors. Thus the conditions in the humus prior to the fire will decide the degree of activation

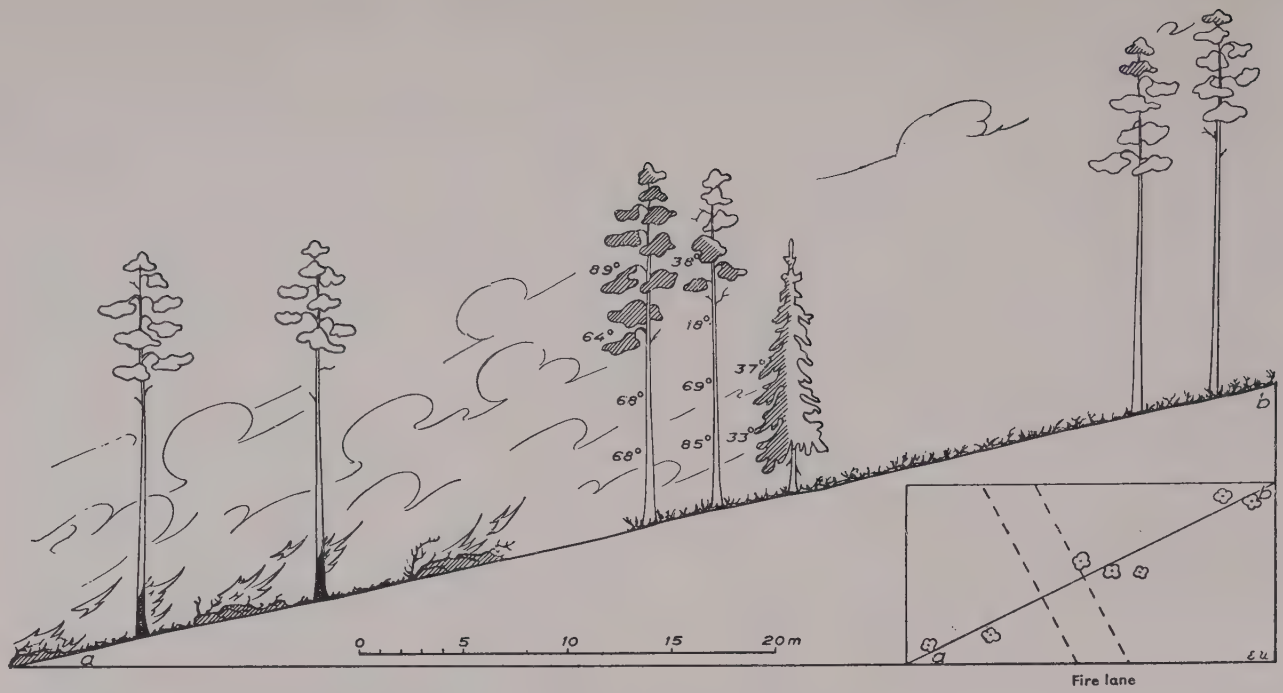

Fig. 2. Diagram of a controlled burning (II p. 465). On the open cut area with the seed-trees (to the left), the strong wind drove the smoke down below the crowns and therefore no damage was observed. The trees behind the fire lane (middle), however, were engulfed in the smoke, and those parts of the crowns subjected to the yellowish-brown to black smoke which resulted from incomplete combustion, were killed (shaded). The temperatures were measured at 3, 6, 8, and 12 m above the ground.

of the soil, and also the duration of the period when conditions in the humus are favourable for the seedlings.

The study of the colonization by individual species was mainly performed in Muddus National Park, but also in connection with the controlled burnings in Hälsingland. Three factors have mainly been taken into consideration: the vegetation before the fire, intensity of the conflagration, and the possibilities of dispersal of the species.

In Hälsingland (II) square-metre plots were marked out and examined before and after the controlled burnings and the plots were then reexamined at fixed intervals. On older cut and burnt areas plots were marked out on severely burnt patches, care being taken to get the plots as similar as possible.

In Muddus National Park (I, III) the immigration of vegetation was examined within fixed sample plots (20 × 25 m) and belt transects of different sizes. The sample plots have been placed in such a way that one of them was as close as possible to the growing forest, the other in the centre of the burnt areas. They were connected by belt transects and the vegetation was analysed according to the HULT–SERNANDER–DU RIETZ five-degree scale (DU RIETZ 1921, p. 225). The seedlings growing within the sample plots and belt transects after the fire have been examined with regard to height, age, type and damage by elk (*Alces alces alces*).[1] Most of the sample plots and belt transects were established in 1945, and have been reexamined in August 1947, 1949, 1953, 1957 and 1958.

The tree layer

Pinus silvestris is Sweden's most fire-resistant tree. Fire scars on old trees in Muddus, especially on pine heaths, show that they have been exposed repeatedly to forest fires without being killed. If, however, the fire is too violent, as in 1933 in Muddus, even the pines on pine heaths are killed.

There exists a tendency towards a coincidence of hot summers, good seed years and years with many forest fires. In Lapland years of regeneration are separated by long intervals.

In northern Sweden the dispersal of *Pinus silvestris* takes place mainly on snowless ground during the months of May and June. On the whole one can say that a border stand can provide seeds satisfactorily, for instance to a burnt area, at a distance from the margin equal to the height of the trees. There are many complicating factors, such as weather, strength and direction of the prevailing winds, turbulence, etc. Also, with increasing distance from the margin of the stand the quality of the seeds becomes poorer and the percentage of empty seeds increases (HEIKINHEIMO 1932, HESSELMAN 1934).

The seeds have a good chance of surviving a not too violent fire, provided that they have lain below the zone of condensation. In connection with the above-mentioned controlled burnings in Hälsingland, the author made experiments with the aim of elucidating the possibility of survival of seeds, by carefully introducing seeds of pine, spruce,

[1] The nearest relation in North America is the moose (*Alces alces americanus*).

and aspen into the humus cover at different depths immediately before the burnings. In one test the temperature during the fire was as high as 438°C at the surface of the soil, but proved to be only 26.5°C at the depth of 3 cm, and 17°C at the depth of 7 cm (II p. 455). The cause of this has been briefly discussed above. The germinative capacity of the seeds which had lain in the humus cover at 3, 5, and 10 cm proved to be as high as that of the untreated control seeds.

The result of the experiments illustrates the high insulating capacity of the humus cover. However, the possibility of these seeds penetrating into the humus is questionable. On dry soils the chances must be considered very small, and only where the vegetation consists, for example, of *Polytrichum commune*, and the soil is thus fairly moist, a very small percentage of these seeds might be able to penetrate into the humus cover deep enough to survive a fire.

The burnt areas in Muddus provide exceptional opportunities for the study of seedlings following dispersal. On an easily reforested heath which burned in 1933 about 5000 pine seedlings per hectare were counted, 24 years after the fire, around isolated pines which had survived, and also close to the border stand. But the dryness on the strongly insolated burnt area, snow blight (*Phacidium infestans*), and other factors, led, however, to the result that, in 1957, out of this large number of seedlings, only about 50 per hectare had reached a height of more than 1.3 m. These seedlings had grown mainly in the shelter of stones and fallen trees, which can offer shadow and where the risk of snow blight is smaller. Towards the centre of the burnt area the number of pine seedlings decreased very rapidly. Thus, 24 years after the fire, there were only about 300 per hectare, and these were mostly less than 10 cm high.

Within one of the burnt areas examined in Muddus the number of seedlings which had been damaged by elks was very large. The investigations corroborate WESTMAN's (1958) results, that an ample supply of deciduous trees—as is the case on burnt areas—does not induce elks to desist entirely from a coniferous diet, and also that elks do not avoid vast reproduction areas.

Also reindeer (*Rangifer tarandus tarandus*) are responsible for damage to the pine seedlings, especially on the heaths of the burnt area of 1933. These heaths are traversed every year in December by Lapps with 20,000–30,000 reindeer on their way down to the forest pastures. In April they return again towards the mountains. At this time the pine seedlings are frozen and brittle, and for this reason part of the damage can be attributed to the trampling of reindeer.

Picea abies very seldom survives a violent forest fire, chiefly because of its thin bark. The seeds of the spruce, being dispersed in late winter and early spring, can be carried for long distances over crusted snow and ice. On this account long-distance dissemination is greater than in pine.

Seedlings of *Picea abies* were, however, almost entirely absent from the investigated

areas in Muddus, even in areas where mixed stands had grown before the fire. The few existing seedlings seemed to suffer from dryness, and there is no doubt that it will be decades, especially within the severely burnt area of 1933, before humus conditions are improved sufficiently for a new reproduction of spruce in the shelter of birch and pine.

Betula pubescens and *B. verrucosa* can spread their light seeds, or rather fruits, over relatively large expanses, especially over burnt areas, which are usually much exposed to the wind. The nut wings of *B. verrucosa* are larger, and as this species often grows in more elevated localities the possibility of dispersal is somewhat greater than in *B. pubescens*.

In literature one often meets the opinion that the "seed" production of birch is more or less constant from year to year. The erroneousness of this statement has been demonstrated e.g. by SARVAS (1948) in southern Finland. The years when "seed" production is large are thus of great importance for the regeneration of birch on burnt areas. The composition of the future forest may be partly determined by the supply of diaspores of pine, spruce and birch in the year following the fire when the soil is most receptive to reproduction.

Sufficient attention has not always been paid to the fact that the two species of birch mentioned have different site demands. *B. verrucosa*, which grows best on drier soil, has a longer lifetime than *B. pubescens*, which demands more moisture. On suitable sites, the growth of *B. verrucosa* is usually faster.

Most of the fruits which germinated after the fire in the layer of ash, e.g. within the burnt area of 1933 in Muddus, were derived from *B. pubescens* which had survived the fire along the watercourses. It could be established that *B. pubescens*, e.g. within a sample plot on the severely burnt area, had decreased between 1945 and 1957 by more than 50 per cent. The corresponding decrease of *B. verrucosa* amounted only to 9 per cent. On dry soils the better initial position of *B. pubescens* with regard to the supply of fruits is thus counterbalanced within a few years by the fact that *B. verrucosa* is growing better upon such soils. Thus in 1957, i.e. 24 years after the fire, all birches higher than 4 m belonged to the species *B. verrucosa*.

In moist localities conditions are entirely different. In belt transects which had been plotted from moist towards dry ground, perpendicularly to watercourses, *B. pubescens* always dominated within the moist part, with a very great number of seedlings. Thus 6 years after the fire a belt transect (5 × 20 m) contained 2839 *B. pubescens*, whereas this species was represented by only 63 seedlings within the drier part. However, after another 6 years, only half of the seedlings survived, partly as a result of natural thinning. Another comparable belt transect (2 × 20 m) contained only 324 birches 16 years after the fire. 8 years later their number had been reduced to 75, only 5 of which were *B. verrucosa*.

The elk does great damage to *B. pubescens* as well as to *B. verrucosa*. The author's investigations have given no support to the old opinion that the elk prefers *B. verrucosa*.

The actual harm is, however, considerably greater as far as *B. verrucosa* is concerned, this species being often commercially more valuable than *B. pubescens*.

Populus tremula can grow on practically any type of soil, but is at its best only on good and well-drained soils. It propagates as a rule by root suckers. The production of suckers is stimulated by forest fires (Lutz 1956). However, on freshly colonized ground, seedlings are not uncommon where the roots of the old aspen have been killed.

Provided that conditions for germination are favourable, the ashes form an excellent seed bed for the small seeds. Under favourable conditions the seeds germinate within 1–2 days. By autumn the seedlings can become 20–30 cm high, and grow very fast during the following few years (Uggla 1957*a*).

The field layer

Arctostaphylos uva-ursi has no subterranean runners and the colonization of burnt areas is effected mainly by seedlings, since the thick-shelled seeds can often survive the fire at a depth of 2–3 cm in the humus cover (Kujala 1926). The fire seems to exert a stimulating influence on the germination, and a great number of seedlings appear in the old localities as early as the summer following the fire.

Calluna vulgaris like *Arctostaphylos* lacks subterranean runners. The small and flat seeds can be spread to a certain extent by the wind, but the faculty of this form of dispersal is too small to explain the occurrence of the great number of seedlings which appear after a fire. We are therefore forced to assume that the seeds can survive the fire in the humus cover, provided that the latter has not been too severely burnt.

Vaccinium myrtillus and *V. vitis-idaea* are able to survive a not too severe fire, due to their richly branched subterranean runners. These are usually embedded in the humus cover at a depth of 2–3 cm where during a fire the rise of temperature does not as a rule amount to many degrees. Thus after a controlled burning (II p. 480) these species had begun to regenerate already some months after the fire in spite of the fact that the temperature at the surface of the soil had risen to 438°C. Under such conditions the species of *Vaccinium* can regain their previous distribution after a few years.

On severely burnt soils, where the subterranean runners have been destroyed by the fire, the regeneration takes a very long time. Seedlings are rare, and only some few specimens have been observed within the burnt areas examined.

Chamaenerion angustifolium belongs to the first colonists on the burnt areas and occurs commonly even in severely burnt spots.

The colonization starts from the usually sterile specimens which generally occur in the old stand. After the fire the subterranean geocorms, which have survived at depths

between 5 and 8 cm, can send up numerous shoots. They reach fertility in quite a short time and supply the burnt area with seeds. Then the seedlings grow very rapidly, and in the summer following the fire in certain cases even reach fertility.

A study of the quantitative development of this species gives a good idea of the nitrogen conditions in the soil. In Muddus the maximum distribution took place about 6 years after the fire and in Hälsingland after about 4 years. Scattered, small, but still flowering specimens were found on the burnt area of 1933 in Muddus as late as 1957.

Deschampsia flexuosa is one of the commonest species on raw humus soils. In Muddus *D. flexuosa* attains its maximum 20 to 30 years after the fire although it behaves very differently on different burnt areas. The shoot system and the relation between the mass of leaves and the flowering shoots is dependent on the site. With increasing development of the young forest it becomes more and more sterile.

Rubus idaeus is favoured by nitrate and appears on most burnt soils a few years after the fire. Seedlings, uniformly spread over the cut area, occurred a few months after a controlled burning (II p. 477). The large number of seedlings indicates that the small fruit-stones had survived the fire in the humus cover below the zone of condensation. The dispersal, which occurs mainly through bird droppings, must have been going on for several years, but the fruit-stones found favourable conditions for germination after the fire had passed over the humus cover.

Further investigations may perhaps show that a certain number of "hard" seeds of this and other species in burnt areas may be brought to germination by high temperature, as is well known in the case of several plants, e.g. *Geranium bohemicum*.

The bottom layer

Ceratodon purpureus, *Polytrichum juniperinum* and *P. piliferum* are characteristic of burnt areas and colonize the bare ground in great numbers.

A distinct difference between the ecological demands of *P. juniperinum* and *P. piliferum* could be observed in burnt areas. The former species was more concentrated around stones and fallen trees, where the conditions of humidity were more favourable, and the latter was more concentrated in drier localities.

In Muddus these mosses culminated about 15 years after the fire. After 24 years they had declined considerably on the burnt area of 1933. In Hälsingland, about 600 km further south, they culminated after only 6 years and were then outgrown by faster-growing mosses.

Hylocomium splendens and *Pleurozium schreberi* are as a rule entirely burnt during a fire, as they often lack connection with the substratum, owing to their mode of growth. Colonization is then very slow. Only when a young stand has grown up again and favour-

able edaphic conditions have thus been established are these mosses able to form a continuous moss cover (C. O. Tamm 1953).

Twenty-four years after the fire *Hylocomium splendens* and *Pleurozium schreberi* were still very rare in the severely burnt area of 1933, and the sample plots did not contain a single specimen. In spite of their probably predominant position in the bottom layer before the fire, it will take several decades before these mosses have again colonized the burnt ground. After a controlled burning the regeneration is faster. Thus *Pleurozium schreberi* had already formed continuous moss cover again 24 years after the burning.

Marchantia polymorpha is amongst the first colonists chiefly on moist, severely burnt soils, and appears in large quantities already one or two years after the fire.

The great competitive ability of *Marchantia* depends partly on the fact that it is not so sensitive to some products released in the dry distillation of wood, which in high concentration has a deadly effect upon most other plants, with the exception of *Funaria hygrometrica* (Lilienstern 1929). As *Marchantia* is favoured by soil humidity, it appears to find its optimum conditions on freshly burnt, moist ground, where the high concentration of lime immediately after the burn is also advantageous for its development.

Two years after the burn *Marchantia* dominated on the most severely burnt spots in the burnt area of 1947 in Muddus. Three years later it had decreased, and was abundantly represented only in moist depressions of the ground.

Species of *Cladonia* occurred sparsely on the heaths within the burnt areas investigated in Muddus. All scientists who have studied the regeneration of the reindeer lichens (*Cladonia* subgenus *Cladina*, i.e. *Cl. alpestris*, *Cl. rangiferina*, *Cl. silvatica*) on burnt areas agree in stating that a very long time is required before they reach their previous quantity (Hustich 1951). This agrees well with the conditions in Muddus. There is no doubt that it will take the reindeer lichens more than 40 years to recover completely, especially in the severely burnt area of 1933, and this applies particularly to *Cl. alpestris*.

The cup-lichens (*Cladonia* subgenus *Cenomyce*) belong to the earlier colonists and were very common on the burnt areas, and 20–30 years after the fire they seem to have regained their original distribution.

*

This brief summary of the occurrence of the different species shows that the vegetation on burnt soils is mostly composed of species immigrating the burnt areas from the surroundings immediately after the fire. For these species, mainly anemochorous, the incinerated part of the humus cover constitutes an excellent seed-bed, provided that the moisture conditions are favourable, and the pH-value not too high. To the anemochores belong, besides the forest trees, e.g. *Chamaenerion angustifolium*.

The other large group is formed by plants which are able to survive the fire in the burnt area. This group in turn can be divided into two parts, one containing species which survive through fructificative diaspores in the humus cover, where the fire may favour their germination. The other consists of species which survive through subterranean parts, for instance runners. To the former group belong e.g. *Arctostaphylos uva-ursi* and *Calluna vulgaris*, to the latter the species of *Vaccinium*.

Some of the species may survive the fire but also colonize the burnt area from outside, e.g. *Populus tremula* and *Chamaenerion angustifolium*.

Certain species, like *Hylocomium splendens* and *Pleurozium schreberi*, rarely survive a forest fire, and are able to form a continuous cover only when the edaphic conditions have become favourable, that is to say, when the young stand has grown up again.

The effect of a forest fire or controlled burning may be very different also within a small area, and a study of the composition of the vegetation permits determinations of the severity of the fire. On the most severely burnt spots anemochores, like *Betula pubescens*, *B. verrucosa*, *Populus tremula*, *Chamaenerion angustifolium*, and *Marchantia polymorpha*, are found. In these spots occur likewise great quantities of *Ceratodon purpureus*, *Polytrichum juniperinum*, and *P. piliferum*.

Along the edges of severely burnt spots *Arctostaphylos uva-ursi* is frequently found. This species has survived in places where the humus cover had been less severely burnt, since its survival, like that of *Calluna vulgaris*, is usually due to seeds in the humus cover. The species which survive by subterranean runners, like *Vaccinium myrtillus* and *V. vitis-idaea*, are almost exclusively found within feebly burnt areas.

THE EFFECT OF FIRE ON THE HUMUS COVER (I–III)

Some chemical changes occurring in the soil after the passage of the fire were studied in Hälsingland, while podsol profiles and the mechanical composition of the soil at different depths were chiefly examined in Muddus.

The samples were taken immediately before and after the burning, and then at different intervals. The decomposition layer and the humus material layer (F- and H-layers) were sampled separately.

On the examined cut areas in Hälsingland the pH in the F-layer varied between 4.1 and 4.5 before the burnings. In samples taken immediately after 7 different burnings the pH values in the F-layer were 6.4, 6.6, 6.7, 6.9, 7.2, 8.4 and 9.5. The last-mentioned sample consisted almost exclusively of ashes from slash. Four samples were taken from the F-layer immediately after the forest fire of 1947 in Muddus, the pH values being 6.1, 7,3, 7.4 and 8.6.

After the controlled burnings also the percentage of calcium, potassium, and phosphorus exhibited a considerable increase. There was a definite connection between the

content of acid-soluble salts of calcium and the pH value both on burnt and unburnt ground. This has been established earlier by several investigators, e.g. Eneroth (1928). Through the burning considerable quantities of calcium are supplied to the soil in a form which is easily available to the plants.

Among the other constituents of the ash, highly soluble salts of potassium and phosphorus predominate. The content of these salts is greatly increased by the burning, but they are also rapidly leached out.

The samples which had been taken at different times after the burnings showed that, in the incinerated part of the decomposition (F) layer, both pH and content of Ca decreased a few months after the burning, and that the leaching of this layer produced a rise in the analytical values in the humus material (H) layer immediately below. Thus 3½ months after a controlled burning the pH value in the F-layer had decreased from 8.4 to 7.0. On an older burnt area the pH in the H-layer was higher than in the F-layer 6 years after the burning. After 10 years the pH values in the humus cover were still higher than normal, and it seems that in the investigated area in Hälsingland about 25 years have to pass before the values become equal to those from adjacent, unburnt, cut areas.

Immediately after the burning, the percentage of total nitrogen had decreased throughout the incinerated part of the humus cover, making it evident that some nitrogen had been lost to the air. This, however, does not seem to be a serious matter in the case of a thick, raw humus cover, where, during the experiments in Hälsingland, only the uppermost part was completely burned. Moreover, most of the nitrogen lost was probably not readily utilizable by plants (Hesselman 1937). Subsequently the percentage of total nitrogen appears to have increased again, and on those areas, which had been cut and burnt long ago, the percentage of total nitrogen was largely the same as for the areas examined before the controlled burnings.

REFERENCES

Arnborg, T., 1951: Om samspelet mellan mark och produktion. En studie av skogen på Bäckmarks hemman i Älvsbyn. (About the interrelation of soil and production.) *Norrl. skogsvårdsförb. tidskr.*, IV. Stockholm.

Du Rietz, G. E., 1921: Zur methodologischen Grundlage der modernen Pflanzensoziologie. Thesis. Uppsala.

Eneroth, O., 1928: Bidrag till kännedom om hyggesbränningens inverkan på marken. (Beiträge zur Kenntnis der Einwirkung des Schlagabbrennens auf den Boden.) *Skogshögskolans festskrift.* Stockholm.

Heikinheimo, O., 1932: Metsäpuiden siementämiskyvystä. I. (Über die Besamungsfähigkeit der Waldbäume. I.) *Comm. Inst. Forest. Fenn.*, 17. Helsingfors.

Hesselman, H., 1934: Några studier över fröspridningen hos gran och tall och kalhyggets besåning. (Einige Beobachtungen über die Beziehung zwischen Samenproduktion von Fichte und Kiefer und der Besamung der Kahlhiebe.) *Medd. fr. Statens skogsforskn.inst.*, 27. Stockholm.

—— 1937: Om humustäckets beroende av beståndets ålder och sammansättning i den nordiska granskogen av blåbärsrik Vaccinium-typ och dess inverkan på skogens föryngring och tillväxt. (Über die Abhängigkeit der Humusdecke von Alter und Zusammensetzung der Bestände im nordischen Fichtenwald von blaubeerreichem Vacciniumtyp und über die Einwirkung der Humusdecke auf die Verjüngung und das Wachstum des Waldes.) *Ibid.*, 30.

Hustich, I., 1951: The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer. *Acta Geographica*, 12. Helsingfors.

Kujala, V., 1926: Untersuchungen über den Einfluss von Waldbränden auf die Waldvegetation in Nord-Finnland. *Comm. Inst. Quaest. Forest. Finl.*, 10. Helsingfors.

Lilienstern, M., 1929: Physiologische Untersuchung über die Ursachen des Vorkommens von Marchantia polymorpha L. auf Feuerstätten. *Ber. d. Deutsch. Bot. Ges.*, XLVII. Berlin.

Lutz, H. J., 1956: Ecological effects of forest fires in the interior of Alaska. *U.S. Dept. of Agr. Techn. Bull.*, 1133. Washington, D.C.

Sarvas, R., 1948: Tutkimuksia koivun uudistumisesta Etelä-Suomessa. (A research on the regeneration of birch in south Finland.) *Comm. Inst. Forest. Fenn.*, 35. Helsingfors.

Tamm, C. O., 1953: Growth, yield and nutrition in carpet of a forest moss (Hylocomium splendens). *Medd. fr. Statens skogsforskn.inst.*, 43. Stockholm.

Uggla, E., 1949: En vegetationsprofil på skogsbrandfält i Muddus nationalpark. (A vegetation analysis in a burnt area in the Muddus National Park.) *Sv. bot. tidskr.*, 43. Uppsala.

—— 1957*a*: Asp och poppel på Mykinge Försöksgård. (Aspen and poplar at Mykinge Experimental Station.) *Lustgården* 1956–1957. Uppsala.

—— 1957*b*: Mark- och lufttemperaturer vid hyggesbränning samt eldens inverkan på vegetation och humus. (Temperatures during controlled burning. The effect on the vegetation and the humus cover.) *Norrl. skogsvårdsförb. tidskr.*, IV. Stockholm.

—— 1958: Skogsbrandfält i Muddus nationalpark. (Forest fire areas in Muddus National Park, Northern Sweden.) *Acta Phytogeogr. Suec.*, 41. Uppsala.

Westman, H., 1958: Älgens skadegörelse på ungskogen. (The damage caused by elk to young stands.) *Kungl. skogshögskolans skrifter*, 28. Stockholm.